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# ON *SOLIDAGO GYPSOPHILA* AND *S. PRINGLEI* (ASTERACEAE: ASTEREAE), RARE AND NOT SO RARE MEXICAN ENDEMICS: A MULTIVARIATE STUDY OF THE *TORTIFOLIA* GROUP OF SUBSECT. *TRIPLINERVIAE*

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## ABSTRACT

Nesom (1989) described *Solidago gypsophila* based on three collections from central Coahuila, Mexico. It is investigated here in a multivariate morphometric analysis that also includes specimens of *S. altiplanities*, *S. altissima* var. *gilvocanescens*, *S. juliae*, *S. leavenworthii*, *S. microglossa*, *S. pringlei*, and *S. tortifolia* (the informal *S. tortifolia* Group) in order to determine similarities among species. Because only one specimen of *S. gypsophila* was scored, it could not be included as an a priori group but it was included in the a posteriori classificatory discriminant analysis and placed in *S. altissima* var. *gilvocanescens* on the basis of upper leaf and floral traits. In a second analysis, including only *S. chilensis*, *S. juliae*, *S. pringlei*, and *S. tortifolia*, the specimen of *S. gypsophila* was placed a posteriori into *S. juliae*, but on the basis of leaf indument traits, phyllary shape, ecology, and distribution it is accepted here as a distinct species. Morphological variation in *S. pringlei* (syn: *S. muelleri*) is also explored and discussed. Detailed illustrations of *S. gypsophila* and *S. pringlei* are presented.

Nesom (1989a) described *Solidago gypsophila* Nesom but did not illustrate the new species. He stated that it was "similar and obviously related to *S. canadensis* var. *canescens* A. Gray in its villous stem pubescence, crowded leaves, large, triangular capitulescence with few disc flowers." Nesom (1989b) treated *S. canadensis* var. *canescens* as a synonym of *S. juliae* Nesom as did Semple & Cook (2006). Upon examining the holotype of *S. gypsophila* (*Henrickson 15576*, LL!), the first author noted similarities of the robust specimen (Fig. 1) to *S. altissima* L. var. *gilvocanescens* (Rydb.) Semple; the leaves (Fig. 2) are much broader than those of *S. juliae* and the inflorescence is broadly secund-conical, while those of *S. juliae* are much narrower. In addition to the short, dense, curved trichomes covering much of the leaf surface, there are also small minute short bumps of unknown composition (Fig. 3). The phyllaries are broader (Figs. 4C-D, 5C) than those of *S. altissima* var. *gilvocanescens* and most other species of *Solidago* subsect. *Triplinerviae* (Torr. & A. Gray) Nesom except for *S. leavenworthii*. Some specimens of *S. pringlei* Fern. and *S. chilensis* Meyen. The rugose venation and surface indument features of *S. gypsophila* are unique to the species in subsect. *Triplinerviae* and the entire genus *Solidago*. Nesom (1989a) was certainly correct in treating *S. gypsophila* as a distinct species.

*Solidago pringlei* Fernald (1901) was described from a collection from Nuevo León, Mexico: (*Pringle 2886*, GH!). Subsequently *Solidago muelleri* Standley (1940) was described from a different collection from Nuevo León (*Mueller 2062*, F!, GH!). Nesom (1989a) treated *S. muelleri* as a synonym of *S. missouriensis* Nutt. in his comments on *Solidago hintoniorum* Nesom, but he annotated the isotype of *S. muelleri* at GH as *S. pringlei* in 1990. A collection from southeast of Galeana, Nuevo León, (*Henrickson 19260,* TEX) was identified on the collection label as *S. altissima*, annotated by B.L. Turner in 1985 as *S. missouriensis*, then annotated by Nesom in 1989 as *S. muelleri* and again in 1990 annotated

as *S. pringlei*. *Nesom & Morgan 5302* (TEX) includes a small shoot and a larger one. Nesom identified the collection on the location label as *S. missouriensis* in 1989 then annotated the sheet as *S. muelleri* in 1989 and then again as *S. pringlei* in 1990. The first author of this paper annotated the larger shoot as *S. pringlei* in 2016 and the smaller one as *S. missouriensis* in 2016. There are not a large number of collections of *S. pringlei* (or *S. muelleri*) in herbaria based on loans requested for this study. Its range is relatively narrow but includes noteworthy variation in stem pubescence densities, numbers of leaf serrations, and in phyllary shape and width. *Solidago pringlei* has been included in subsect. *Triplinerviae* by Nesom (1994) and by Semple (2016, frequently updated).

In order to explore morphological similarities and differences among *Solidago gypsophila* and likely related species, a multivariate morphometric comparison of *S. gypsophila* and *S. altissima* var. *gilvocanescens* was undertaken and included specimens of *S. altiplanities* Taylor & Taylor, *S. juliae, S. leavenworthii* Torr. & A. Gray, and *S. tortifolia* Ell. from the southcentral and southeastern USA., *S. pringlei* from Mexico, and *S. chilensis* Meyen and *S. microglossa* DC. from South America. These species have been grouped into the informal *Tortifolia* Group by Semple (2016, frequently updated). The results of the analysis are presented below. These analyses also allowed comparisons of *S. pringlei* with other related species.

## Nomenclature

**Solidago gypsophila** Nesom, Phytologia 67: 142. 1989 **TYPE**: **MEXICO**. **Coahuila**. Mpio. Cuatro Cienegas, ca 9 air mi SW of Cuatro Cienegas, ca 2 mi N of Poza Becerra, in a fen-like area, with *Flaveria, Baccharis, Sciprus, Anemopsis, Sporobolus, Distichlis*, coarse perennial, lvs gray-green, fls yellow, 26° 52' N, 102° 08' W, 709 m, 10 Oct 1976, *J. Henrickson 15576* with M. Dillon (holotype: LL!, Figs. 1-4).

Additional collections examined: **MEXICO**. **Coahuila**. Mpio. Cuatro Ciene Grande, Cuatro Cienegas Basin, small laguna between Lagunas Churince and Grande, 13 Aug 1967, *Cole, Minckley, & Pinkava 3790* (ASU!, almost in flower, disc florets corollas not open); Dos Quatos, 21 Aug 1967, *Cole, Minckley & Pinkava 4336* (ASU!, immature, very small inflorescence buds present).

**Solidago pringlei** Fern., Proc. Amer. Acad. Arts 36: 505. 1901. **TYPE**: **MEXICO**. **Nuevo León**. Near Monterey, Sierra Madre, 22 Aug 1889, *C.G. Pringle 2886* (holotype: GH!, Fig. 5).

*Solidago muelleri* Standl., Field Mus. Pub. Bot. 22: 128. 1940. **TYPE**: **MEXICO**. **Nuevo León**. Mpio. de Villa Santiago, Cañon Marisio Abajo, Rancho Las Adjuntas, common in moist crevices on river bank, f.c. deep yellow, 27 Jun 1935, *C.H. Mueller 2062* (holotype: F 888438!, Fig. 6; isotypes: GH!, MICH digital image!, MO digital image!).

Additional collections examined: **MEXICO**. **Coahuila**: Sierra la Gavia, Rancho la Gavia, 25 Oct 1995, *Villarreal & Carranza 3366* (TEX). **Nuevo León**: near Monterey, Sierra Madre, 12 Aug 1889, *Pringle 1586* (MEXU); Sierra Madre near Monterrey, 22 Aug 1889, *Pringle 2586* (MEXU PVT33274, digital image); Mpio. Galeana, 10 km E of Galeana, Pocitos, 26 Aug 1984, *Hinton 18780* (UNAM Herb Hinton, digital image), Enramadas, 20 Mar 1992, *Hinton 21858* (UNAM Herb. Hinton, digital image); Montemorelos, at La Trinidad, 10 Aug 1988, *Patterson 6434* (TEX); 5 km S Galeana, near concrete bridge 0.5 km to E of main road, 31 Nov 1985, *Nesom & Morgan 5302* (TEX); ca 15 air km SE of Galeana, just S of Cerro Potosí at old abandoned settlement at Santa Rita de Cardeladas, 10 Oct 1982, *Henrickson & Hess 19260* (TEX); Santa Rita, 23 Mar 1993, *Hinton 22721* (TEX, UNAM Herb. Hinton, digital image); above Santa Rita, 12 Jan 1989, *Hinton 19300* (UNAM Herb. Hinton, digital image); Villa de Santiago, Las Adjuntas, 21 Jun 1940, *Leavenworth 180* (GH, TEX); Rio Ramos near Los Adjuntas, in Sierra Madre, 5 Sep 1992, *Soule, Patterson, & LeDuc 3263* (TEX); Santa Rita, 23 Mar 1993, *Hinton et al. 19300* (TEX); N of La Trinidad on road from [Portrero] Redondo, 5 Sep 1992, *Soule, Patterson, & LeDuc 3289* (TEX).

**Figure 1**. Holotype of *Solidago gypsophila* (*Henrickson 15576*, LL).

**Figure 2.** Details of holotype of *Solidago gypsophila*: stem and leaves. **A-B.** Lower mid stem. **C.** Upper stem. **D.** Lower mid stem leaf. **E.** Upper leaf. **F-G.** Lower mid stem leaf apex and margin, abaxial face. **H-J.** Upper leaf, abaxial face, upper mid-section, aveolae, proximal mid vein and prominent lateral veins. Scale bar = 1 cm in D and E; = 1 mm in A-B, F, G-J.

**Figure 3.** Detail of holotype of *Solidago gypsophila*: abaxial face of upper mid-section of upper leaf. Scale bar = 1 mm.

### Multivariate Analysis

## MATERIALS AND METHODS

In total, 216 specimens from BM, BRIT, F, FSU, GH, the J.K. Morton personal herbarium now deposited in ROM, K, LL, LP, MADM, MEL, TEX, USF, and WAT in MT (Thiers, continuously updated) were scored and included in the analysis. Data on *Solidago chilensis* (92 specimens), *S. juliae* (11 specimens), *S. leavenworthii* (15 specimens), *S. microglossa* (31 specimens), and *S. tortifolia* (16 specimens) were measured by the second author for her M.Sc. thesis (Lopez Laphitz 2009) and in Lopez Laphitz and Semple (2011), except for a few specimens scored by the author since 2009. Data on *S. altiplanities* (9 specimens) and *S. altissima* var. *gilvocanescens* (29 specimens) were previously used in Semple et al. (2015). New data on *S. gypsophila* (one specimen) and *S. pringlei* (12 specimens) were scored for this study by the first author. For each specimen, 13 vegetative and 16 floral traits were scored when possible: 1-5 replicates per character depending upon availability of material and whether or not the trait was meristic (Table 1). Mean values were used in the analyses, while raw values were used to generate ranges of variation for each trait. All traits scored are listed in Table 1. Phyllary width traits were not scored on specimens of *S. altissima* var. *gilvocanescens* and were scored on only two specimens of *S. altiplanities.*

Traits used to define a priori groups were not included in the analyses to avoid circular logic. Differences in general inflorescence shape and branching characteristics, lower stem pubescence density, and leaf pubescence density were used to define a priori groups along with geographic location. Lower stem leaf traits were not included in the analyses because these were often not present on specimens.

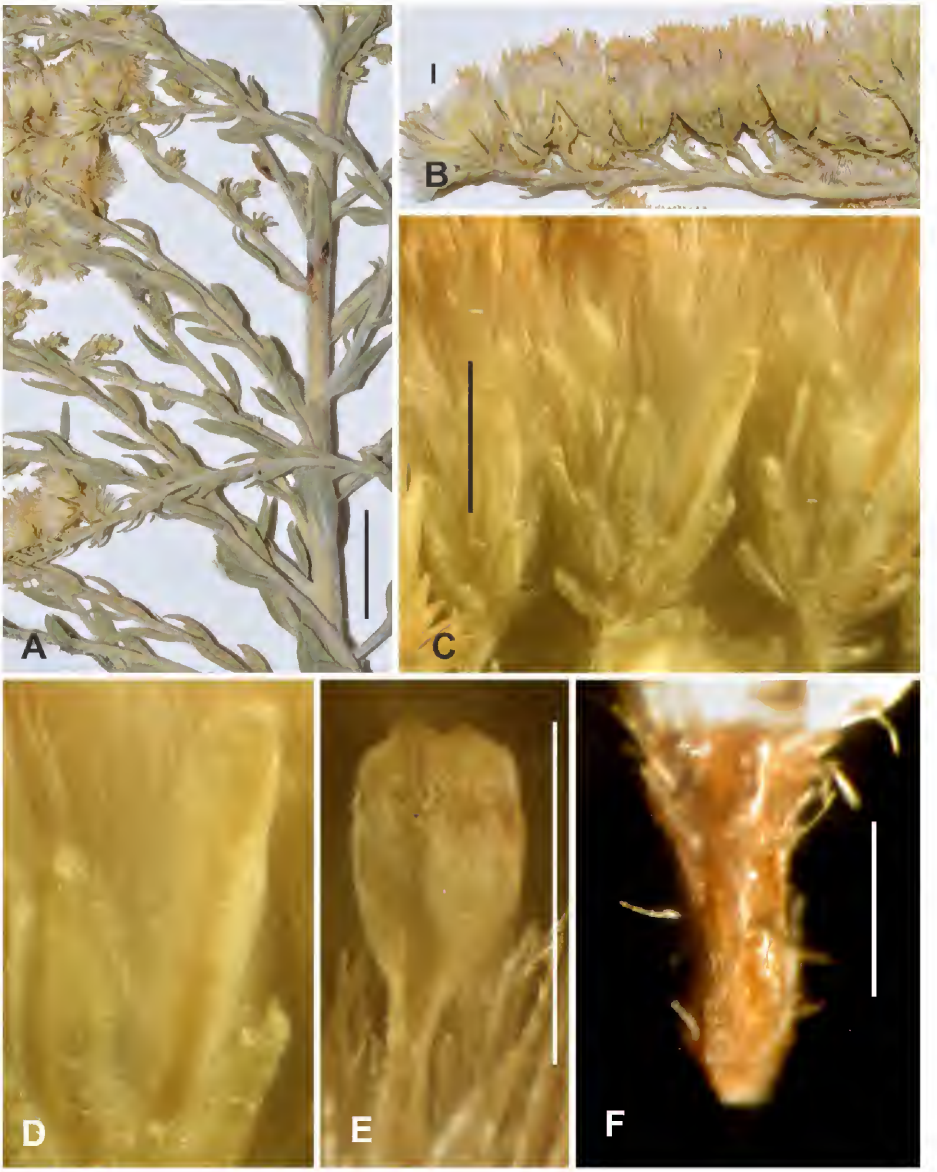


**Figure 4**. Details of holotype of *Solidago gypsophila*: inflorescence, heads and florets. **A.** Upper mid portion of inflorescence. **B.** Heads of lower branch of inflorescence. **C.** Involucres. **D.** Mid and inner phyllaries. **E.** Ray floret lamina. **F.** Immature cypsela body (ca. 0.5 mm long). Scale bar = 1 cm in A; = 1 mm in B, C, E; = 0.5 mm in F.

**Figure 5.** Details of *Solidago gypsophila* (*Cole, Minckley, & Pinkava 3790*, ASU). **A-B.** Inflorescences. **C.** Phyllaries. Scale bar = 1 cm in A-B; = 1 mm in C.

**Figure 6.** Holotype of *Solidago pringlei* (*Pringle 2886*, GH).

TYPE
888438
PLANTS OF MEXICO
STATE OF NUEVO LEON
Solidago Muelleri Standl., sp. nov.
HOLOTYPE: Solidago muelleri Standl., Field Mus. Pub. Bot. 22: 128. 1940. MEXICO. NUEVO LEON. Mpio. de Villa Santiago, Rancho Las Adjuntas, Cañon, Margen Abajo, common in moist crevices on river bank, fr deep yellow, 27 Jun 1935, Mueller 2062 (HT: F[888438]; IT: GH!, MICH, MO)
John C. Semple 13 April 1991
University of Waterloo, WAT

**Figure 7.** Holotype of *Solidago muelleri* (*Mueller 2062*, F).

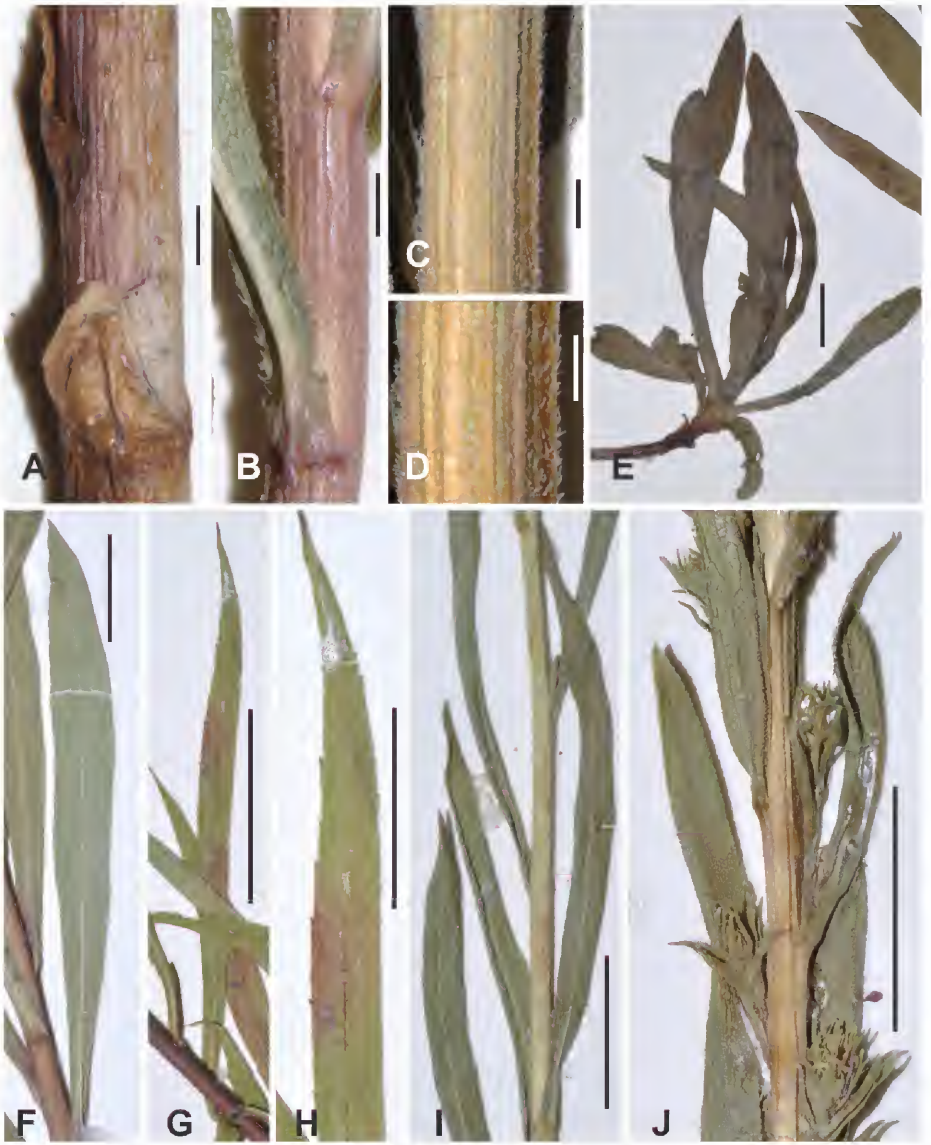


**Figure 8.** Details of *Solidago pringlei*: stem and leaves. **A-B.** Lower and mid stems, *Leavenworth 180* (GH). **C-D.** Upper stem, *Nesom & Morgan 5302* (TEX). **E.** Rhizome and new shoot leaves, *Hinton 21858* (TEX). **F.** Lower stem leaf, *Hinton 22721* (TEX). **G-H.** Mid stem leaf and apex, *Patterson 6434* (TEX). **I.** Upper stem and leaves, *Villareal 8366* (TEX). **J.** Leaves, base of inflorescence, *Henrickson & Hess 19260* (TEX). Scale bar = 1 mm in A-D; = 1 cm in E-J.

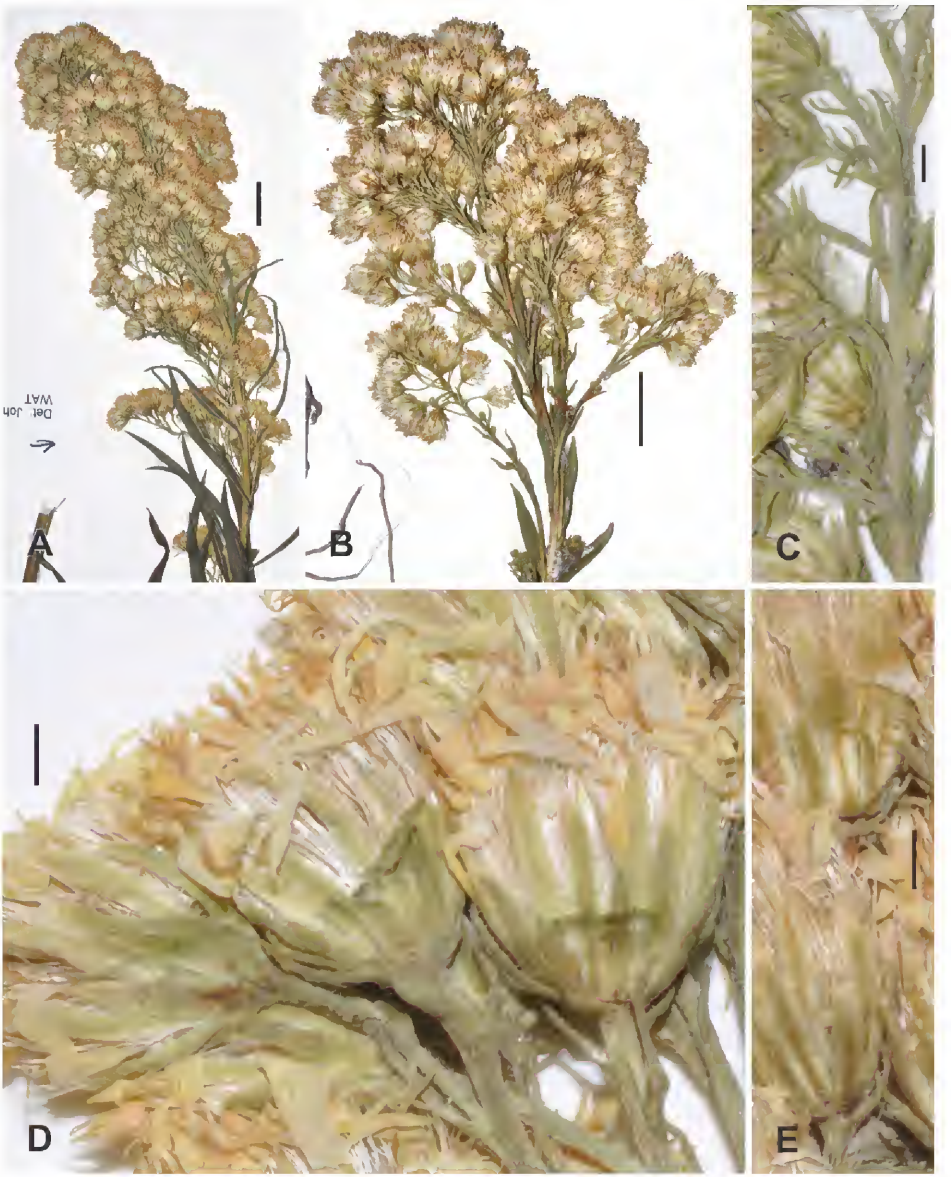


**Figure 9**. Details of *Solidago pringlei*; inflorescences, heads, florets. **A-B**. Inflorescences, *Nesom & Morgan 5302* (TEX) and *Henrickson & Hess 19260* (TEX). **C.** Peduncles and bracts, *Soule et al. 3263* (TEX). **D.** Heads with lanceolate phyllaries, *Hinton 22721* (TEX). **E.** Heads with some oblong phyllaries, *Hinton 19300* (TEX). Scale bar = 1 cm in A-B; = 1 mm in C-E.

Table 1. Traits scored for the multivariate analyses of specimens of *Solidago altiplanities*, *S. chilensis*, *S. gypsophila*, *S. juliae*, *S. leavenworthii*, *S. microglossa*, *S. pringlei*, and *S. tortifolia*.

| Abbreviation | Description of trait scored |
|---|---|
| STEMHT | Stem height measured from the stem base to tip(cm) |
| LLFLN | Lower leaf length measured from the leaf base to tip(mm) |
| LLFWD | Lower leaf width measured at the widest point (mm) |
| LLFWTOE | Lower leaf measured from the widest point to the end(mm) |
| LLFSER | Lower leaf dentation-number of serrations of lower leaf |
| MLFLN | Mid leaf length measured from the leaf base to tip (mm) |
| MLFWD | Mid leaf width measured at the widest point (mm) |
| MLFWTOE | Mid leaf measured from the widest point to the end (mm) |
| MLFSER | Mid leaf dentation-number of serrations of mid leaf |
| ULFLN | Upper leaf length measured form the leaf base to tip( mm) |
| ULFWD | Upper leaf width measured at the widest point (mm) |
| ULFWTOE | Upper leaf measured from the widest point to the end(mm) |
| ULFSER | Upper leaf dentation-number of serrations of upper leaf |
| CAPL | Length of inflorescence (cm) |
| CAPW | Width of inflorescence (cm) |
| INVOLHT | Involucre height (mm) |
| OPHYLN | Outer phyllary length (mm) |
| OPHYLW | Outer phyllary width (mm) |
| IPHYLN | Inner phyllary length (mm) |
| IPHYLW | Inner phyllary width (mm) |
| RAYNUM | Number of ray florets per head |
| RSTRAPLN | Ray strap length top of the corolla tube to the tip of the strap (mm) |
| RSTRAPWD | Ray strap width measured at the widest point (mm) |
| RACHLN | Ray floret cypsela body length at anthesis (mm) |
| RPAPLN | Ray floret pappus length at anthesis (mm) |
| DCORLN | Disc corolla length from the base to tip of the corolla lobes (mm) |
| DLOBLN | Disc corolla lobe length lobe (mm) |
| DACHLN | Disc achene length (mm) |
| DPAPLN | Disc pappus length (mm) |

All analyses were performed using SYSTAT v.10 (SPSS Inc. 2000). A pair-wise Pearson correlation matrix was created to determine which characters were highly correlated. One trait of each pair that had a $> |0.7|$ correlation value was excluded from the analysis to avoid possible pleiotropic effects of a single gene and to make the tests of null hypotheses more stringent. Stepwise discriminant analysis (STEPDISC) was used to select traits that best separated groups based on the Mahalanobis distances between a priori group centroids in N-dimensional hyperspace. Classificatory discriminant analysis was run on N-1 traits selected by the STEPDISC analysis, if more than N-1 traits were selected, where N = lowest sample size of the a priori groups; in this study N=9 (*Solidago altiplanities*). A COMPLETE analysis was then run using only eight traits. Geisser probabilities of assignment to each a priori group were generated for each specimen a posteriori based on the Mahalanobis distances from the specimen location plotted in N-dimensional hyperspace to each a priori group centroid. Linear and

Jackknifed analyses were run in each classificatory analysis to test the strength of group separation in terms of the numbers of discriminating traits. Results are presented in the form of (1) F-value matrices based on Mahalanobis distances between group centroids and (2) tables summarizing the results of the two methods of doing the classificatory discriminant analyses. Conclusions were reached based on the percents of correct placements of specimens and the probabilities of the placements being correct and visual re-examination of each specimen via high resolution digital images or the actual specimens. Lastly, a canonical analysis was performed as a dimension reduction technique to allow visualization of results in 1 to 3 dimensions with the number of dimensions being N-1, where in this case N equals the number of a priori groups in an analysis. While canonical analysis allows for a visual presentation of results, the plots are based on fewer axes than are used in the statistical analyses and thus do not fully show the multi-dimensional nature of the separation of a priori groups.

Two analyses were performed. One included all taxa and all specimens scored. A second analysis was run on just specimens of *Solidago chilensis*, *S. juliae*, *S. pringlei*, and *S. tortifolia* as four a priori groups and the one specimen of *S. gypsophila* a posteriori. This was done because the species are all diploids and whose members were sometimes misplaced into the other taxa in the eight-group analysis. Any influence of ploidy level would be avoided by including only these taxa. *Solidago microglossa* was excluded because its distinctive long pubescence was not seen in the Mexican species.

## RESULTS

### Eight-taxa analysis

In the COMPLETE discriminant analysis of seven species level a priori *Solidago altiplanities*, *S. altissima* var. *gilvocanescens*, *S. chilensis*, *S. juliae*, *S. leavenworthii*, *S. microglossa*, *S. pringlei*, and *S. tortifolia*, the following eight traits were used from a longer list selected in a preliminary STEPWISE analysis and are listed in order of decreasing F-to-remove values: number of ray florets (19.09), involucre height (15.99), mid leaf width (14.59), mid leaf serrations (9.97), number of disc florets (7.14), mid leaf length (6.56), ray floret cypsela pappus length at anthesis (5.81), and ray floret lamina length at anthesis (0.80). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 2. F-values based on Mahalanobis distances between group centroids indicated the largest separations were between *Solidago altissima* var. *gilvocancens* and the two South American species *S. chilensis* and *S. microglossa* (48.541 and 30.768, respectively) and the least separation was between *S. juliae* and *S. torifolia* (3.692).

In the a posteriori Classificatory Discriminant Analysis of the eight-species level a priori groups plus the one specimen of *Solidago gypsophila, S. altiplanities* was the only a priori group with 100% placement to that group a posteriori; a posteriori assignments for other groups ranged from 67-94% to their own group (Table 3). The Classification matrix and Jackknife classification matrix are presented in Table 3.

**Table 2.** Between groups F-matrix for the eight a priori group analysis (df = 8, 7, 204).

| Group | *altiplanities* | *altissima gilvocan.* | *chilensis* | *juliae* | *leaven-worthii* | *micro-glossa* | *pringlei* |
|---|---|---|---|---|---|---|---|
| ***alt. gilvocan.*** | 13.958 | | | | | | |
| ***chilensis*** | 10.958 | 48.541 | | | | | |
| ***juliae*** | 7.429 | 4.984 | 11.763 | | | | |
| ***leavenworthii*** | 11.329 | 19.645 | 9.535 | 8.103 | | | |
| ***microglossa*** | 16.532 | 30.768 | 7.633 | 9.141 | 8.485 | | |
| ***pringlei*** | 8.874 | 15.794 | 10.977 | 4.360 | 6.167 | 13.525 | |
| ***tortifolia*** | 6.689 | 9.953 | 32.573 | 3.692 | 19.033 | 28.952 | 11.590 |

Wilks' lambda = 0.0609 df = 8 7 207; Approx. F = 13.1661 df = 56 1082 prob = 0.0000

**Table 3.** Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of eight a priori groups; a posteriori placements to groups in rows.

| Group | *altiplan-ities* | *altissima gilvocan.* | *chilensis* | *juliae* | *leaven-worthii* | *micro-glossa* | *pringlei* | *torti-folia* | % correct |
|---|---|---|---|---|---|---|---|---|---|
| ***altiplanities*** | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 100 |
| ***alt. gilvocan.*** | 0 | 25 | 0 | 2 | 0 | 0 | 0 | 2 | 86 |
| ***chilensis*** | 5 | 1 | 62 | 1 | 7 | 12 | 4 | 0 | 67 |
| ***juliae*** | 0 | 2 | 0 | 8 | 1 | 0 | 0 | 0 | 73 |
| ***leavenworthii*** | 0 | 0 | 3 | 3 | 9 | 0 | 0 | 1 | 60 |
| ***microglossa*** | 0 | 0 | 5 | 1 | 2 | 23 | 0 | 0 | 74 |
| ***pringlei*** | 1 | 0 | 0 | 2 | 0 | 1 | 8 | 0 | 67 |
| ***tortifolia*** | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 15 | 94 |
| **Totals** | 15 | 29 | 70 | 17 | 19 | 36 | 12 | 17 | 74 |

Jackknifed classification matrix

| Group | *altiplan-ities* | *altissima gilvocan.* | *chilensis* | *juliae* | *leaven-worthii* | *micro-glossa* | *pringlei* | *torti-folia* | % correct |
|---|---|---|---|---|---|---|---|---|---|
| ***altiplanities*** | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 100 |
| ***alt. gilvocan.*** | 0 | 25 | 0 | 2 | 0 | 0 | 0 | 2 | 86 |
| ***chilensis*** | 6 | 1 | 57 | 1 | 7 | 15 | 5 | 0 | 62 |
| ***juliae*** | 0 | 2 | 0 | 8 | 1 | 1 | 0 | 0 | 73 |
| ***leavenworthii*** | 0 | 0 | 3 | 4 | 7 | 1 | 0 | 1 | 47 |
| ***microglossa*** | 0 | 0 | 5 | 2 | 2 | 22 | 0 | 0 | 71 |
| ***pringlei*** | 1 | 0 | 0 | 2 | 0 | 1 | 8 | 0 | 67 |
| ***tortifolia*** | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 15 | 94 |
| **Totals** | 16 | 29 | 65 | 19 | 174 | 39 | 13 | 17 | 70 |

Results are presented in decreasing order of percent correct placement. Eight of nine specimens of *Solidago altiplanities* were placed a posteriori into the *altiplanities* group with 90-100% probability; one was placed into the group with 71% probability (19% to *S. tortifolia*, 6% to *S. juliae*, and 3% to *S. pringlei*). Fifteen of 16 specimens of *S. tortifolia* (94%) were assigned a posteriori to the *S. tortifolia* group; 9 with 90-96% probability, 4 with 81-87% probability; 2 with 73% and 67% probabilities. One *S. tortifolia* specimen was placed into the *S. altissima* var. *gilvocanescens* group with 85% probability (6% to *S. juliae*, 4% to *S. microglossa*, 2% to *S. tortifolia*, and 1% to *S. leavenworthii*). Twenty-five of the 29 specimens of *S. altissima* var. *gilvocanescens* (86%) were assigned a posteriori to the *S. altissima* var. *gilvocanescens* group; 15 with 90-100% probability, 6 with 76-88% probability; 3 with 51-53% probability. Four *S. altissima* var. *gilvocanescens* specimens were placed into other species groups: 2 into *S. tortifolia* with 80% and 63% and 2 into *S. juliae* with 59% probability (14% *S. altissima* var. *gilvocanescens*) and 37% (24 % to *S. altissima* var. *gilvocanescens*, 24% to *S. pringlei*, and 13% to *S. altiplanities*). Twenty-three of the 31 specimens of *S. microglossa* (74%) were assigned a posteriori to the *microglossa* group; 7 with 94-99% probability, 7 with 71-81% probability; 6 with 60- 66% probabilities, and 3 with 50-55% probability. Eight *S. microglossa* specimens were placed a posteriori into other species groups: 5 were placed in the *S. chilensis* group with 57-78% probability, 2 were placed in the *S. leavenworthii* group with 88% and 36% probabilities, and 1 was placed in the *S. juliae* group with 59%. Eight of 11 specimens of *S. juliae* (83%) were assigned a posteriori to the *S. juliae* group: 4 with 81-88% probability, 2 with 70-71% probability, and 2 with 65-65% probability. Three specimens of *S. juliae* were placed a posteriori into two other taxa: 2 were placed into *S. altissima* var. *gilvocanescens* with 85% probability and 50% probability (29% to *S. juliae*, 11% to *S. pringlei*, 5% to *S. tortifolia* and 4% to *S. leavenworthii*), and 1 specimen was placed into *S. leavenworthii* with 56% probability (32% to *S. pringlei*, 7% to *S. juliae*, and 4% to *S. altissima* var. *gilvocanescens*). Sixty-two of 92 specimens of *S. chilensis* (67%) were assigned a posteriori to the *S. chilensis* group; 7 with 90-96% probability, 16 with

80-87% probability; 9 with 70-79% probability, 13 with 60-69% probability, and 17 with 39-59% probability. Thirty specimens of *S. chilensis* (including most of the adventive specimens to other parts of the world) were placed a posteriori into other species: 10 specimens were placed into the *S. microglossa* group with 28-73% (14-46% to *S. chilensis*), 6 into the *S. leavenworthii* group with 37-87% probability (17-46% to *S. chilensis*); 5 into *S. altiplanities* with 52-95% probability, 2 into *S. pringlei* with 32% and 86% probabilities, and 1 into *S. juliae* with 51% probability (34% to *S. chilensis*, 16% to *S. microglossa*, and 4% to *S. pringlei*). Eight of 12 specimens of *S. pringlei* (67%) were assigned a posteriori to the *S. pringlei* group; 4 with 95-99% probability and 4 with 65-79% probability. Four *S. pringlei* specimens were placed into other species: 2 into *S. juliae* with 59% and 61% probabilities (38% and 27% to *S. pringlei*, 8% and 1% to *S. tortifolia* and *S. microglossa*, respectively), 1 to *S. microglossa* with 63% probability (36% to *S. chilensis*, and 1% to *S. pringlei*), and 1 to *S. altiplanities* with 59% probability (20% to *S. chilensis*, 12% to *S. pringlei* and 5% to *S. juliae*). Nine of 15 specimens of *S. leavenworthii* (60%) were assigned a posteriori to the *S. leavenworthii* group; 3 with 98-100% probability, 5 with 79-88% probability; and 1 with 37% probability (35% to *S. microglossa*, 10% to *S. juliae*, and 9% to *S. chilensis*). Six *S. leavenworthii* specimens ware placed into other species: 3 to *S. chilensis* 93%, 92% and 56% probability (27% to *S. leavenworthii*, 13% to *S. microglossa*, and 3% to *S. leavenworthii*). The holotype specimen of *S. gypsophila* which was not assigned to an a priori group was assigned a posteriori to *S. altissima* var. *gilvocanescens* with 73% probability (21% to *S. juliae* and 6% to *S. tortifolia*).

Two dimensional plots of CAN1 versus CAN 3 and CAN1 versus CAN2 canonical scores for specimens of *Solidago altiplanities*, *S. chilensis*, *S. juliae*, *S. leavenworthii*, *S. microglossa*, *S. pringlei*, and *S. tortifolia*, and the single collection of *S. gypsophila* are presented in Fig. 7. The positions of the *S. gypsophila* specimen on the two plots are indicated by yellow stars. Eigen values on the first three axes were 2.835, 0.813 and 0.488.

**Four-species analysis**

In the STEPWISE discriminant analysis of four-species level a priori groups (*Solidago chilensis*, *S. juliae*, *S. pringlei*, and *S. tortifolia*) and the one specimen of *S. gypsophila* included a posteriori, the following eight traits were selected and are listed in order of decreasing F to remove values: involucre height (13.60), number of ray florets (12.94), disc floret cypsela pappus length at anthesis (10.72), mid leaf length (7.47), mid leaf width (6.75), disc achene body length at anthesis (5.54), outer phyllary width at widest point (3.99), and disc floret corolla lobe length (3.94). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of $p = 0.000$ that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 4. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between *Solidago chilensis* and *S. tortifolia* (24.110) and the small separation was between *S. juliae* and *S. pringlei* (3.067).

In the Classificatory Discriminant Analysis of the four-species level a priori groups plus the one specimen of *Solidago gypsophila* a posteriori, all 11 specimens of *S. juliae* (100%) were assigned to that species a posteriori: 4 with 92-94% probability, 3 with 81-86% probability, and 4 with 77%, 70%, 62% and 54% (42% to *S. pringlei*). The Classification matrix and Jackknife classification matrix are presented in Table 5. Seventy-nine of 84 specimens of *S. chilensis* (94%) native to South America were assigned a posteriori into the *S. chilensis* group; 57 with 92-100% probability, 7 with 80-89% probability, 12 with 65-77% probability, and 2 with 50-52% probability. Five specimens were assigned a posteriori to other species: 3 to *S. juliae* with 84%, 72% and 70% probabilities and 2 to *S. pringlei* with 65% and 61% probabilities. Fourteen of the 15 specimens of *S. tortifolia* (93%) were assigned a posteriori into the *S. tortifolia* group; 12 with 94-100% probability, and 2 with 89% and 78% probabilities. One specimen was assigned a posteriori to *S. juliae* with 60% probability (37% to *S. tortifolia*, 3% to *S. pringlei*). Eleven of the 12 specimens of *S. pringlei* (92%) were assigned a posteriori to the *S. pringlei* group; five with 93-99% probability (including the holotype) and 3 with probabilities of 85%, 67%, and 59% (38% to

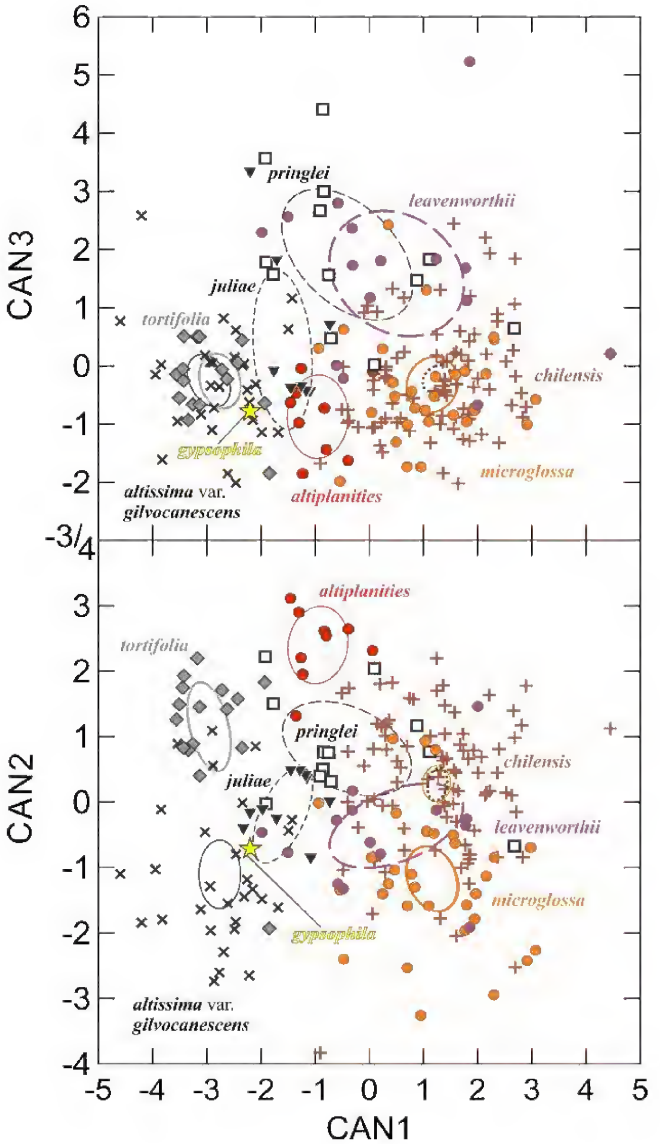


**Figure 10.** Plots of CAN1 versus CAN3 and CAN1 versus CAN2 of 212 specimens of *Solidago altiplanities* (red dots), *S. altissima* var. *gilvocanescens* (black ×), *S. chilensis* (brown +), *S. juliae* (black triangles), *S. leavenworthii* (purple dots), *S. microglossa* (orange dots), *S. pringlei* (white squares with black outlines), *S. tortifolia* (gray diamonds with black outlines), and the one collection of *S. gypsophila* (yellow star); 95% confidence ellipses are included.

*S. juliae*). One specimen, the GH isotype of *S. muelleri*, was assigned a posteriori to the *S. juliae* group with 53% probability (42% to *S. pringlei*, 5% to *S. tortifolia*). The single specimen of *S. gypsophila* was assigned a posteriori to *S. juliae* with 95% probability (4% to *S. tortifolia* and 1% to *S. pringlei*).

Two dimensional plots of CAN1 versus CAN 3 and CAN1 versus CAN2 canonical scores for specimens of *Solidago chilensis*, *S. juliae*, *S. pringlei*, *S. tortifolia*, and the single collection of *S. gypsophila* are presented in Fig. 11. The positions of the *S. gypsophila* specimen on the two plots are indicated by yellow stars. Eigen values on the first three axes were 3.545, 0.438, and 0.178.

**Table 4.** Between groups F-matrix for the four a priori group analysis (df = 8, 7, 204).

| Group | *chilensis* | *juliae* | *pringlei* |
|---|---|---|---|
| ***juliae*** | 6.946 | | |
| ***pringlei*** | 8.930 | 3.067 | |
| ***tortifolia*** | 24.110 | 4.047 | 7.556 |

Wilks' lambda = 01021 df = 14 3 118
Approx. F= 8.6018 df = 42 312 prob = 0.0000

**Table 5.** Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of four a priori groups; a posteriori placements to groups in rows.

| Group | *chilensis* | *juliae* | *pringlei* | *tortifolia* | % correct |
|---|---|---|---|---|---|
| ***chilensis*** | 79 | 3 | 2 | 0 | 94 |
| ***juliae*** | 0 | 11 | 0 | 0 | 100 |
| ***pringlei*** | 0 | 1 | 11 | 0 | 92 |
| ***tortifolia*** | 0 | 1 | 0 | 14 | 93 |
| **Totals** | 79 | 16 | 13 | 14 | 94 |

Jackknifed classification matrix

| Group | *chilensis* | *juliae* | *pringlei* | *tortifolia* | % correct |
|---|---|---|---|---|---|
| ***chilensis*** | 78 | 4 | 2 | 0 | 93 |
| ***juliae*** | 0 | 9 | 2 | 0 | 82 |
| ***pringlei*** | 1 | 3 | 8 | 0 | 67 |
| ***tortifolia*** | 0 | 2 | 0 | 13 | 87 |
| **Totals** | 79 | 18 | 12 | 13 | 89 |

## DISCUSSION

The results of the multivariate analyses support the recognition of *Solidago altiplanities*, *S. chilensis*, *S. gypsophila*, *S. juliae*, *S. leavenworthii*, *S. microglossa*, *S. pringlei*, and *S. tortifolia* as separate species and *S. altissima* var. *gilvocanescens* as a separate taxon. Because a single specimen cannot be treated as an a priori group in discriminant analyses, the single specimen of *S. gypsophila* was not assigned to an a priori group but was included in the a posteriori classificatory discriminant analyses, which assigned a posteriori the specimen in the eight-species analysis to *S. altissima* var. *gilvocanescens* with 73% probability (21% to *S. juliae*, 6% to *S. tortifolia*) and in the four-species analysis to *S. juliae* with 95% probability. In both analyses, involucre height and numbers of ray florets were the two most important traits in separating the a priori groups, with the two traits switching first and second position in importance in the two analyses.

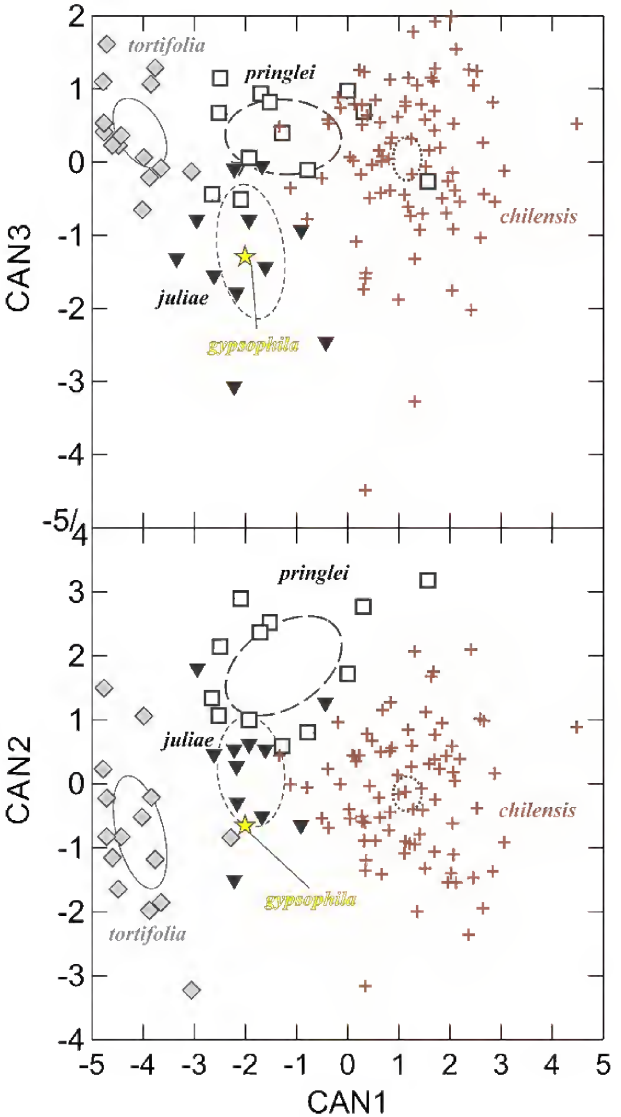


**Figure 11.** Plots of CAN1 versus CAN3 and CAN1 versus CAN2 of 119 specimens of *Solidago chilensis* (brown +), *S. juliae* (black triangles), *S. pringlei* (white squares with black outlines), and *S. tortifolia* (gray diamonds with black outlines), and the one collection of *S. gypsophila* (yellow stars); 95% confidence ellipses are included.

The results support Nesom's (1989a) observation that *Solidago gypsophila* is similar to *S. juliae* (treated in that paper as *S. canadensis* var. *canescens*) and the initial observation of the first author of this paper that *S. gypsophila* was similar in some ways to *S. altissima* var. *gilvocanescens.* The broad middle

and inner phyllaries of *S. gypsophila* separate the species from both *S. juliae* and *S. altissima*, although the trait was not selected by STEPDISC as significant in separating a priori groups in both the eight- and four-taxa analyses. The holotype of *S. gypsophila* has a very robust long branched inflorescence, while the nearly flowering paratype illustrated in Fig. 5 has smaller and short branched inflorescences that are like those of most specimens of the *Tortifolia* Group, i.e., long and narrow secund-conical inflorescences, which is a more accurate description than the often used "secund-pyramidal" description.

This is the first multivariate analysis that has included *Solidago pringlei* and all eight of the core informal *Tortifolia* group of species in subsect. *Triplinerviae.* Lopez Laphitz (2009) and Lopez Laphitz and Semple included six of the species in the analyses focusing on the two South American species *S. chilensis* and *S. microglossa.* Semple et al. (2015) included *S. altiplanities* and *S. juliae* in their analysis of *S. altissima* and *S. canadensis* varieties. The results of both the eight-species analysis and the four-species analysis of this paper demonstrate that the northeastern Mexican endemic *S. pringlei* is central to the *Tortifolia* group of species because it includes variation in traits that are useful in defining other species. Lower stem pubescence varies from typical-for-the-group very short densely villose-canescent indument to glabrous, which occurs generally in *S. chilensis* from Chile and central and southern Argentina. Broader phyllaries are typical in *S. leavenworthii* and occur in some *S. chilensis*, both of which have taller involucres, but they are most pronounced in *S. gypsophila* because it has shorter involuces and shorter phyllaries. Of note, some specimens of *S. pringlei* were assigned to *S. chilensis* in the eight- species analysis. The first author's initial impression of the loan of specimens from TEX was that there might be two separate taxa in the stack of 10 specimens. Preliminary results did not support this, and all collections were treated as belonging in a variable *S. pringlei* that included some specimens that were rather *S. chilensis*-like. The GH holotype of *S. pringlei* was placed a posteriori into *S. pringlei* (95% and 97% probabilities). In both analyses, the GH isotype of *S. muelleri* was placed a posteriori into *S. juliae* with 61% probability (27% to *S. pringlei*, 8% to *S. tortifolia*) in the eight-species analysis and 53% (42% to *S. pringlei*, 5% to *S. tortifolia*) in the four-species analysis. However, on the basis of stem pubescence it does not belong in that species and does look overall similar to some specimens of *S. pringlei* that were included in the species a posteriori. Based on the holotype and the isotypes, *S. muelleri* should be treated as a synonym of *S. pringlei.*

*Solidago pringlei* is a likely candidate for the species that was long-distance dispersed from northern Mexico to Bolivia, where it diverged and evolved into *S. chilensis* and *S. microglossa.* The alternative to this interpretation is that *S. chilensis* was introduced into Nuevo León, Mexico, in post Columbian times and persisted long enough to hybridize with *S. pringlei* at some locations to add more *S. chilensis*-like features to some *S. pringlei*, but never became well established as it has in the West Indies and other locations. Parsimony favors the idea that *S. pringlei* is simply rather variable in stem indument and phyllary traits.

The known chromosome numbers for *Solidago altiplanities*, *S. chilensis*, *S. microglossa*, and *S. tortifolia* are all diploid, $2n$=18. *Solidago leavenworthii* includes tetraploids and hexaploids. The chromosome numbers of *S. gypsophila* and *S. pringlei* are unknown.

The eight species analysis does not provide evidence that *Solidago altissima* var. *gilvocanescens* is a member of the *Tortifolia* group of species of subsect. *Triplinerviae,* which generally have narrow lanceolate to linear lanceolate leaves and narrow elongated secund conical inflorescences. A multivariate analysis of all species of subsect. *Triplinerviae* is needed. In the eight-species analysis presented here, *S. altissima* var. *gilvocanescens* was most distant from *S. chilensis* and *S. microglossa* but not close to *S. juliae*, as indicated by Mahalanobis distances and the accompanying F-to-separate values. A molecular phylogeny of all species in the genus with data sufficient to resolve relationships of closely related species is very much needed. Multivariate analysis is not a method suited for determining phylogenetic relationships, although it can reveal morphological similarities previously overlooked.

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